
SYSTEMATICS AND CHROMOSOME CYTOLOGY OF *ELEUTHERINE* HERBERT (IRIDACEAE)¹

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ABSTRACT

The New World genus *Eleutherine* (Iridaceae, tribe Tigridieae) is treated as comprising two species that are characterized by a bulbous rootstock, a large subapical cauline leaf, and small, white, stellate, evening-blooming flowers. The more common *E. bulbosa* (syn. *E. plicata*) extends across South America from Bolivia and southeastern Brazil to the West Indies and is widely cultivated for its medicinal properties. Less well known is *E. latifolia* (here including *E. citriodora*), with centers in northern Central America and subtropical South America. Both species have a basic chromosome number of $x = 6$ ($2n = 12$) and a similar bimodal karyotype, which is distinctive in Tigridieae; all other genera of the tribe have $x = 7$. The common form of *E. bulbosa* has a heteromorphic long chromosome pair, the result of a pericentric inversion in one of the long chromosomes, and it is sexually sterile, unlike *E. latifolia*, which is self-compatible and autogamous. The systematics and nomenclature of the two species are dealt with in detail, and the medicinal properties of *E. bulbosa* are outlined.

Eleutherine Herbert (1843), a member of the New World tribe Tigridieae of Iridaceae, comprises low-growing bulbous plants with pleated lanceolate leaves and small, white, evening-blooming flowers. *Eleutherine bulbosa* (Miller) Urban (syn. *E. plicata* (Sw.) Klatt), which extends across South America from Bolivia and southeastern Brazil to the West Indies, has been known since the seventeenth century (Baker, 1892). Currently, Ravenna (1984a) admits two more species, *E. latifolia* (Standley & L. O. Williams) Ravenna of northern Central America and subtropical South America, and *E. citriodora* (Ravenna) Ravenna, from northern Argentina. We recognize only *E. latifolia* and suggest that *E. citriodora* is conspecific with *E. latifolia*. Two more species have been described from Indochina (Gagnepain, 1934), both conspecific with *E. bulbosa*. They are sometimes erroneously thought to be native there and are still occasionally recognized (Schultes, 1990).

The two species of *Eleutherine* are alike in their nearly identical small, white, stellate flowers with free, ascending stamens and relatively long, filiform style arms that extend between the anthers. Vegetatively they share two unusual features, both synapomorphies: a large foliage leaf inserted at the apex of the vegetative part of the stem; and dark

red, rather than brown, bulb scales. In other vegetative features, *Eleutherine* accords well with Tigridieae in having a true bulb and plicate foliage leaves, two important synapomorphies for the tribe (Goldblatt, 1990). The common cultivated strain of *E. bulbosa* is sexually sterile for reasons outlined below. It comprises part of the pharmacopeia of several America Indian tribes and may be a clone that has been dispersed by humans from a source in the eastern Andean foothills of Peru, where the most fertile of the few capsulate specimens occur.

In this paper we describe the chromosome cytology of *Eleutherine* and provide evidence that although both species appear to have an unspecialized morphology, the genus is likely to be a derived genus of Tigridieae. A key to the species, complete nomenclature, and descriptions of the species are provided in the systematics section.

MATERIALS AND METHODS

Collections of *Eleutherine* were obtained from wild sources (Table 1) and cultivated at the Missouri Botanical Garden. For cytological study, root tips were pretreated in aqueous m-bromonaphthalene for 4 hours and then fixed in 3 : 1 absolute ethanol-

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TABLE 1. Chromosome numbers and collection data for species of *Eleutherine* studied. Voucher specimens are located at the Missouri Botanical Garden (MO).

Species	Diploid number	Collection data
<i>E. latifolia</i>	12	Argentina. Tucumán: <i>Castillo</i> sub <i>Goldblatt</i> 9072
	12	Mexico. San Luis Potosí: Tamazunchale, Howard sub <i>Goldblatt</i> 9071
<i>E. bulbosa</i>	12	Peru. Loreto: Pampa Hermosa and vicinity, <i>Lewis et al.</i> 10624

glacial acetic acid. After hydrolysis in 10% HCl for 6–7 minutes at ca. 65°C, root tips were squashed in FLP orcein (Jackson, 1972). Karyotypes were drawn with a camera lucida.

Notes on reproductive biology were based on observation of fruit set in greenhouse plants that were not accessible to potential insect pollinators.

OBSERVATIONS

Two populations of *Eleutherine latifolia*, one from Argentina and one from Mexico, are self-fertile, seed-producing plants with a diploid chromosome number of $2n = 12$. They have an identical karyotype (Fig. 1A, C) of one long subtelo-centric chromosome pair 5–6 μm long (including secondary constrictions), and five much shorter, submetacentric to acrocentric pairs 1.5–2 μm long. Large satellites are located on the very small short arms of the two long chromosomes. The satellites are ca. 1 μm long and much exceed the short arms of the long chromosomes. Although easily overlooked in contracted metaphase preparations, they are a striking characteristic of the karyotype. In prophase, the satellites are easily mistaken for a

pair of small chromosomes. The thin secondary constrictions are difficult to see and are sometimes stretched by manipulation during preparation of squashes such that the satellites lie some distance from the arms to which they are attached.

Plants of *Eleutherine bulbosa* from Peru, apparently sexually sterile, have a karyotype similar to the above *except* that the pair of long chromosomes do not match. The long arms and satellites differ in length (Fig. 1B). The total length of the chromosomes is, as far as we can estimate by linear measurement of camera-lucida-drawn chromosomes, close to, if not the same as the *E. latifolia* populations. Thus, the longer satellite is ca. 2.3 μm long, and the rest of the chromosome including the secondary constriction is ca. 3.5 μm long. The chromosome with the short satellite is ca. 6 μm long, including the satellite, which is ca. 1 μm long, and corresponds in length and morphology to the long chromosomes of *E. latifolia*.

DISCUSSION

CYTOGENETICS

The chromosomes of *Eleutherine latifolia* accord well with those of *E. bulbosa* in the basic features of the karyotype, $x = 6$ with extreme bimodality and a strongly acrocentric long chromosome pair to which are attached large satellites. The karyotype was briefly described by Guerra (1988), based on unpublished observations of A. Kenton, but a detailed description and illustration have not been published until now.

The basic features of the karyotype of *Eleutherine bulbosa* (also reported in the literature as *E. plicata*) are already known (Zaman et al., 1985; Cherian & Kuriachan, 1988—based on plants cultivated in India; Martinez & De Azkue, 1987; Guerra, 1988—based on plants of South American

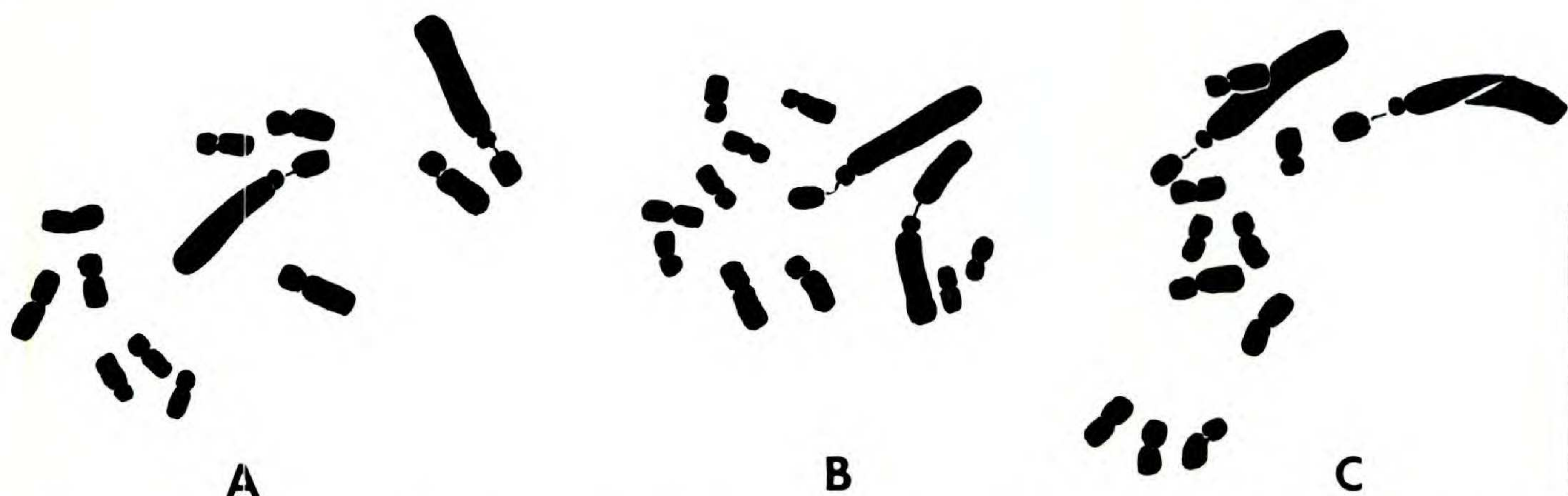


FIGURE 1. Karyotypes of *Eleutherine latifolia* from Mexico (A) and Argentina (C), and *E. bulbosa* (B). (Scale bar = 5 μm .)

origin). *Eleutherine guatemalensis* Standley, which has $2n = 28$ (Ravenna, 1965), is now *Cobana guatemalensis* (Standley) Ravenna. The genus *Cobana* is probably not closely related to *Eleutherine* and belongs in Tigridiinae rather than Cipurinae, where *Eleutherine* seems well placed (Goldblatt, 1982).

The earliest chromosome counts in the literature for *Eleutherine bulbosa* are those of Sharma & Talukdar (1959) and Rao (1969), both papers reporting $2n = 14$ and a karyotype of two long pairs of chromosomes, one of which is metacentric. In the same paper, Sharma & Talukdar (1959) reported $2n = 12$ (and 14) in *Cipura paludosa* Aublet; their drawings of the chromosomes of the two species make it clear that their plants were misidentified. The karyotypes of their so-called *Eleutherine* closely match published karyotypes for *Cipura paludosa* (e.g., Goldblatt, 1982), whereas the karyotypes of their cytotypes of *C. paludosa* correspond with *Eleutherine* here, with some minor variation. The plants studied by Rao (1969) as *Eleutherine* were presumably also misidentified, and their count of $2n = 14$ must be ignored. (*Cipura*, especially *C. paludosa*, is understandably confused with *Eleutherine*, but the two genera are probably not immediately related.)

Subsequently, Goldblatt (1982) reported $2n = 12$ and a structurally heterozygous karyotype in *Eleutherine bulbosa*. Zaman et al. (1985) also found $2n = 12$ in *E. bulbosa*, and they reported regular bivalent formation at meiosis and the presence of an inversion bridge with a fragment at meiosis I. Based on this, they postulated that a pericentric inversion in one of the two long chromosomes was responsible for the long chromosome heteromorphism. A fragment associated with a meiotic bridge is not compatible with a pericentric inversion (cf. Stebbins, 1971), but Zaman et al.'s interpretation of the meiotic figures, not illustrated, may not have been correct. A study by Guerra (1988) finally demonstrated convincingly the presence of a pericentric inversion in one of the long chromosomes of *E. bulbosa*, and he also reported a small tandem duplication of part of the short arm of the chromosome with the inversion (and longer satellite), rendering this chromosome slightly longer than its homologue. Guerra's conclusions make the comments of Cherian & Kuriachan (1988) on the nature of the chromosomal restructuring in *E. bulbosa* redundant and need not be repeated here. Despite their refutation of the presence of a pericentric inversion in the species, the meiotic configurations illustrated in their paper show the bridges formed by the long chromosomes without

fragments, consistent with heterozygosity for a pericentric inversion.

It is virtually certain that the ancestral karyotype in *Eleutherine* had $x = 6$ and was structurally homozygous, as described here in *E. latifolia* and likely to occur in sexually reproducing *E. bulbosa*, not yet examined cytologically. The mismatched long chromosome pair in the cultivated strain of *E. bulbosa* has a pericentric inversion, which is responsible for its sexual sterility; this accounts for the absence of capsules on most herbarium material of *E. bulbosa* and in cultivated plants. Fertile populations and at least partially fertile individuals do, however, exist. A collection from Peru (*Schunke 971*, NY, F) comprises several individuals, all bearing numerous capsules. Other collections comprise at least one plant with a few developed capsules (*Duss 3836* from Guadelupe, US; *Costa 164* from Pará, Brazil, F; *Faris 475* from Santo Domingo, US). The capsules are small and globose and differ from those of *E. latifolia*, which are oblong to cylindrical and always substantially larger.

The basic chromosome number for the entire Tigridaeae is probably $x = 7$ (Goldblatt, 1982, 1990; Kenton & Rudall, 1987), and there are few exceptions in the tribe. Only *Gelasine elongata* (Graham) Ravenna (syn. *G. azurea* Herbert fide Ravenna, 1984b) also has $n = 6$ ($2n = 12$) (Kenton & Rudall, 1987). The chromosome number is known in only one other *Gelasine*, *G. uruguayensis*, which has $n = 7$ (Ravenna, 1984c). The karyotype of *G. elongata* has a long acrocentric chromosome pair with conspicuous satellites larger than the short arms (misinterpreted by Goldblatt, 1982, as a pair of small chromosomes), and in this respect resembles *Eleutherine*. However, *G. elongata* differs in having a second relatively long chromosome pair. The karyotype of *G. elongata* is structurally heterozygous, and the chromosomes form a ring of 12 at meiosis (Kenton & Rudall, 1987). Karyotypic and cytogenetic differences between *Eleutherine* and *Gelasine elongata* make it seem unlikely that the two share an immediate common ancestor. The $n = 6$ in *G. elongata* most likely originated from ancestors within the genus with $x = 7$. The only other member of Tigridaeae that is known to diverge from the basic $x = 7$ is *Cypella plumbea* Lindley, $n = 5$, but other species of the genus have $n = 7$, which is the basic number for *Cypella* (Goldblatt, 1982; Kenton & Heywood, 1984).

SYSTEMATICS AND PHYLOGENY

The two species that we propose to recognize in *Eleutherine* have virtually identical flowers, but

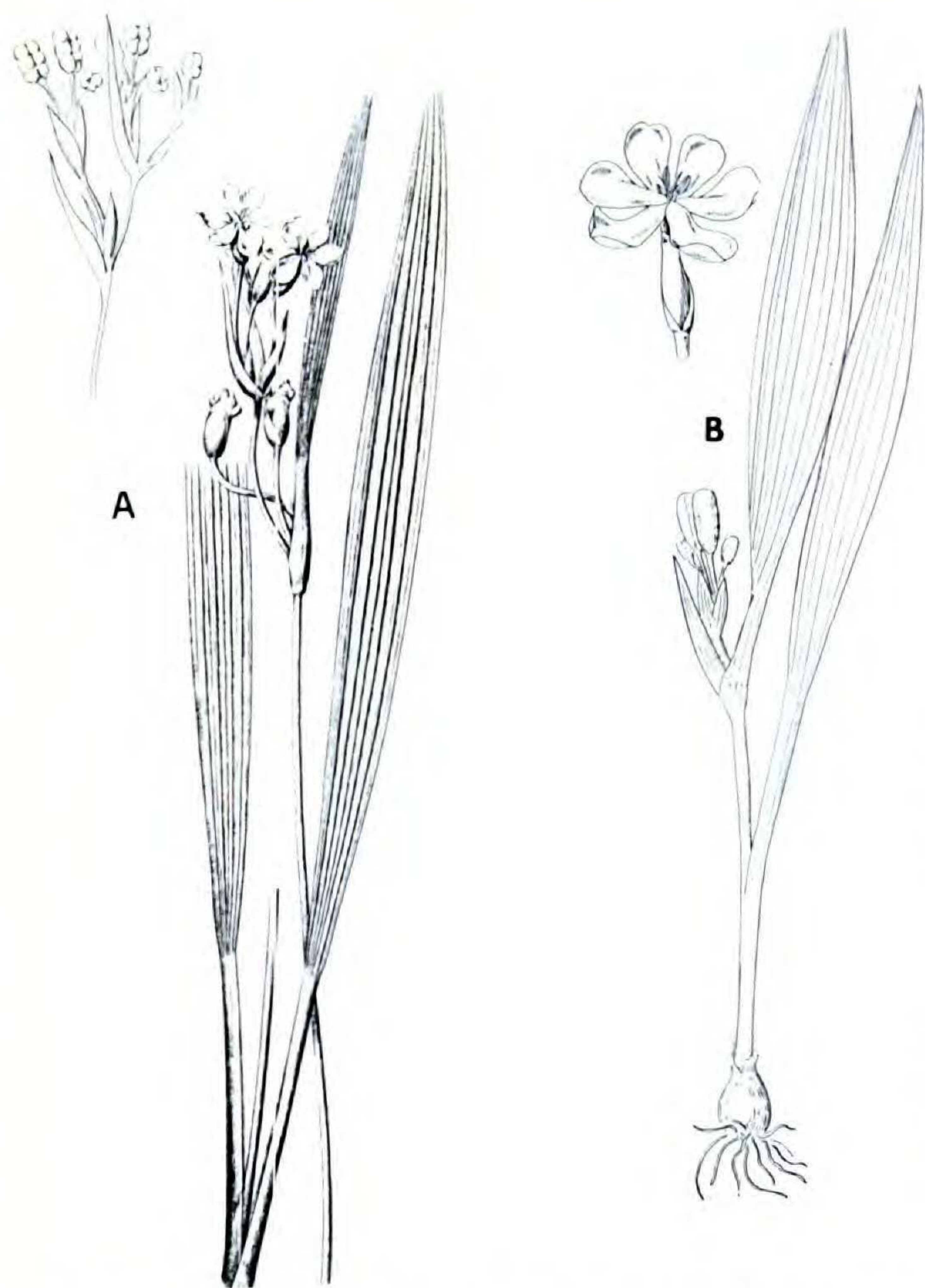


FIGURE 2. Morphology of *Eleutherine bulbosa* (A) and *E. latifolia* (B). Habits $\times 0.5$, flower and fruiting branch of *E. bulbosa* full size.

they are readily distinguished by differences in their inflorescence structure (Fig. 2). In *E. latifolia*, generally a short plant, the large apical cauline leaf subtends one or sometimes two sessile to shortly pedunculate rhipidia (spathe-enclosed flower clusters), the basic inflorescence type in Iridaceae (Fig. 2B). In *E. bulbosa* the cauline leaf subtends a few pedunculate rhipidia and a secondary axis that terminates in (3–)6–12 rhipidia in umbellate arrangement; thus the rhipidia are arranged in two series, axillary and terminal (Fig. 2A).

The flowers of *Eleutherine* (Fig. 3A) appear to be relatively simple in structure and comparable with those of more primitive genera of Iridaceae. It is tempting to interpret the genus as primitive within Tigridaeae, in which a more complex flower structure is the rule. However, Mariceae, sister tribe of Tigridaeae, are also characterized by a complex flower structure (Fig. 3B) almost identical with that of Tigridaeae (Goldblatt, 1990; Goldblatt & Henrich, 1991), in which the tepals are clawed, the inner tepals have a zone of nectariferous tissue in a fold of the tepal limb, and the thickened style branches are terminally bifurcate and have a sub-

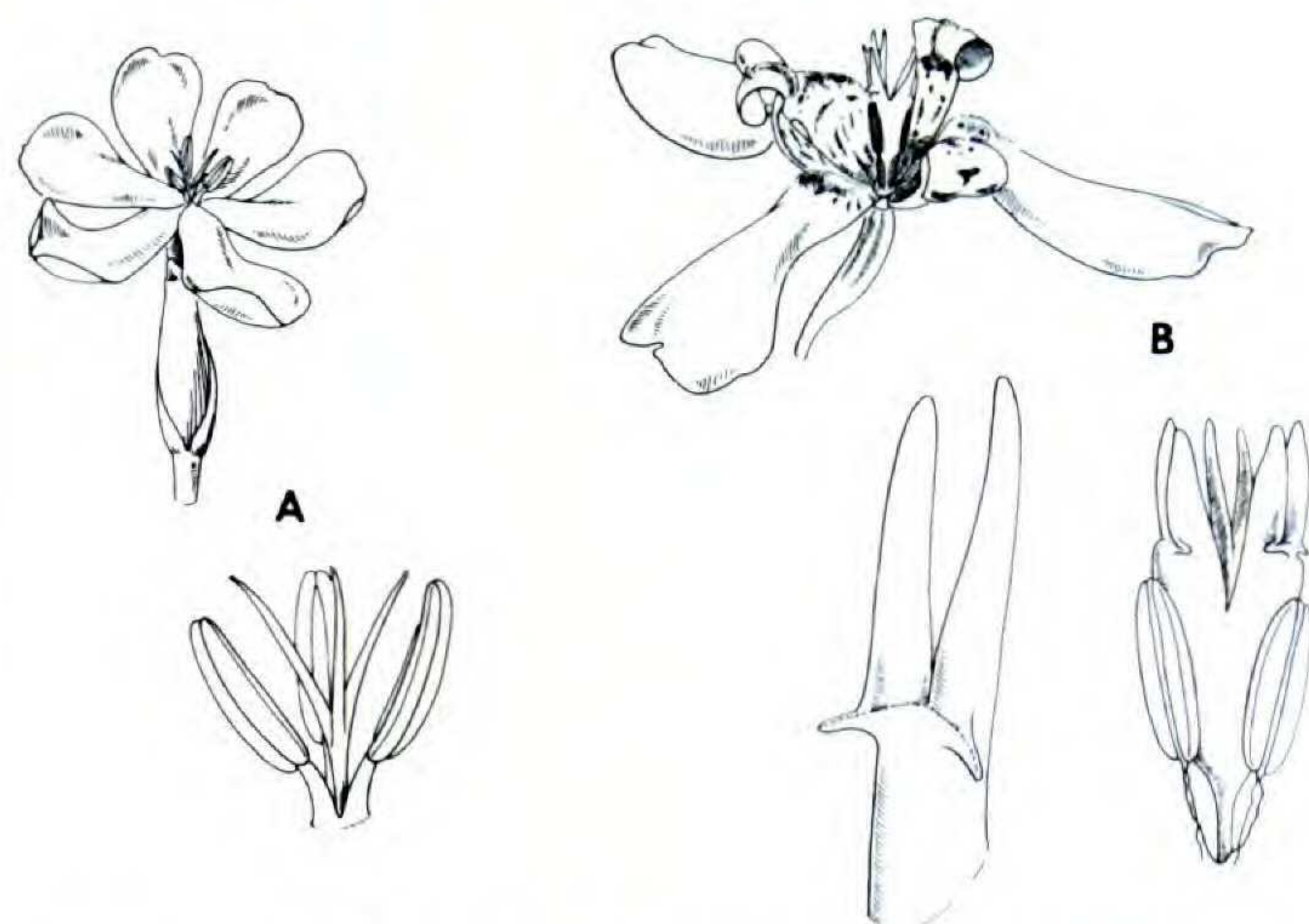


FIGURE 3. Details of the flowers and stamens and style of *Eleutherine* (A) and of the putative ancestral type represented by *Trimezia steyermarkii* (B). Whole flowers full size; details of the separated stamens and styles and style branches much enlarged.

apical transverse stigma. It seems more parsimonious to interpret the flower of *Eleutherine* as derived by a process of reduction in complexity associated with self-compatibility and autogamy, a derived type of reproductive biology in Tigridaeae that is basically self-incompatible (Goldblatt, pers. obs.). Similar examples of the simplification of an ancestrally complex flower structure are known within Iridaceae in tribe Irideae, notably in subtribe Homeriinae (Goldblatt, 1979, 1981, 1986). Here, flowers with clawed tepals and elaborate petaloid, apically bifurcate style arms with transverse stigmas, are believed to have been secondarily reduced in several lineages, leading in one genus, *Roggeveldia* Goldblatt, to species with stellate flowers with simple filiform style branches that alternate with the stamens.

SYSTEMATICS

Eleutherine Herbert, Edwards's Bot. Reg. 29: t. 57 (1843). TYPE: *E. plicata* Herbert (= *E. bulbosa* (Miller) Urban).

Galatea Salisb., Trans. Hort. Soc. 1: 310 (1812), nom. nud.

Small, seasonal perennials with a fleshy bulb with reddish tunics. Leaves few, plicate, both basal and cauline, narrowly lanceolate. Stem terete, comprising one long internode, with a large cauline leaf at the apex, subtending the inflorescence. Inflorescences rhipidia, these solitary or several and then arranged in a pseudopanicule; rhipidia (spathe-enclosed umbels) several-flowered, stalked or \pm sessile; spathes green, subequal, relatively short. Flower pedicellate, subtended by membranous

bracts as long as the spathes; perianth white, stellate; tepals free, subequal, spreading from the base, without nectaries; filaments free; anthers diverging. Ovary obovoid; style short and dividing opposite the upper half of the filaments, the branches undivided, filiform, extending between the anthers, stigmatic apically. Capsules globose to oblong-cylindrical, truncate; seeds angular. Basic chromosome number $x = 6$.

Eleutherine consists of two species distributed in Mexico, West Indies, Central and South America; cultivated in Africa and Asia, especially the Philippines and Indochina, and now naturalized there.

KEY TO THE SPECIES

- 1a. Plants with several rhipidia per flowering stem, the peduncles borne both in the axils of the cauline leaf and in umbellate fashion on a secondary axis; rarely setting fruit, but capsules globose, 4–6.8 mm long 1. *E. bulbosa*
- 1b. Plants with 1 or rarely 2 rhipidia either \pm sessile or borne on short peduncles inserted in the axil of the cauline leaf; always setting fruit and capsules 12–20 mm long 2. *E. latifolia*

1. ***Eleutherine bulbosa*** (Miller) Urban, Rept. Spec. Nov. Regni Veg. 15: 305 (1915). Basionym: *Sisyrinchium bulbosum* Miller, Gard. Dict. ed. 8 (1768). *Galatea bulbosa* (Miller) Britton, Brooklyn Bot. Gard. Mem. 1: 37 (1918) nom. inval., gen. inval. TYPE: uncertain, possibly figure in Burman, Pl. Amer. Fasc. 35 & t. 46 f. 2 (1757 as 1755), but not specifically cited by Miller [perhaps a neotype should be chosen]. [Miller may have had living plants but cited Tournefort, Inst. Rei Herb. 387 (1700), who in turn cited Magnol, Hort. Reg. Monsp. (1697), neither of which has any illustration of the species nor refers to one]. Figure 2A.

Ixia americana Aublet, Hist. Pl. Guiana 1: 33 (1775). *Galatea americana* (Aublet) Kuntze, Revis. Gen. Pl. 2: 701 (1891) nom. inval., gen. inval. *Sisyrinchium latifolium* Sw., Prodr. 17 (1788) nom. illeg. superfl. *Moraea plicata* Sw., Fl. Ind. Occid. 1: 82 (1797) nom. illeg. superfl. *Marica plicata* (Sw.) Ker-Gawler, Curtis's Bot. Mag. 18: t. 665 (1803). *Galatea vespertina* Salisb., Trans. Hort. Soc. 1: 310 (1812) nom. inval., gen. inval. *Cipura plicata* (Sw.) Griseb., Fl. Brit. W. Indian Is. 589 (1864). *Eleutherine* (as *Eleutherina*) *plicata* (Sw.) Klatt in Martius, Fl. Bras. 3(1): 514 & t. 64, f. 2 (1871). TYPE: illustration in Burman, Pl. Amer. Fasc. 35 & t. 46 f. 2 (1757 as 1755).

Eleutherine anomala Herbert, Edward's Bot. Reg. 29: t. 57 (1843). *Galatea anomala* (Herbert) Kuntze,

Revis. Gen. Pl. 2: 701 (1891) nom. inval., gen. inval. TYPE: illustration in Bot. Reg. 29: t. 57.

Eleutherine subaphylla Gagnepain, Bull. Soc. Bot. France 81: 66 & f. 67. 1934 et in Fl. Gen. de l'Indo-Chine 6: 676. 1934. TYPE: Vietnam (Annam, Quang-Tri), *Poilane* 12279 (P) (a form flowering without basal leaves).

Eleutherine longifolia Gagnepain, Bull. Soc. Bot. France 81: 66. 1934 et in Fl. Gen. de l'Indo-Chine 6: 677. 1934. TYPE: Vietnam (Annam, ? Hué), *Jacquet* 611 (P) (described from vegetative plants).

Sisyrinchium americanum, *radice phaenicea*, *foliis plicatis & nervosis etc.*, Magnol, Hort. Reg. Monsp. 185 (1697).

Bermudiana palmaefolio, *radice bulbosa* Tournefort, Inst. Rei Herb. 1: 388 (1700).

Sisyrinchium palmifolium sensu Lam., Encyc. Méth. 1: 408 (1783-85) et sensu Cavanilles, Diss. 6: 348 & t. 191 (1788) non Linnaeus, Mantissa Pl. 122 (1767) (= *S. palmifolium* L.). (Also *Moraea palmifolia* sensu Jacquin, Icon. Pl. Rar. 2: t. 227 (1790), non sensu Linnaeus; *Eleutherine palmifolia* sensu Merrill, Philipp. J. Sci. 7: 233 (1912) non sensu Linnaeus).

Plants 15–75 cm high, usually sexually sterile and lacking capsules; other characters as for the genus except the following. Inflorescence of several stalked rhipidia, the peduncles borne both in the axil of the cauline leaf and in umbellate fashion on a secondary axis; spathes 11.5–15(–20) mm long; peduncles (12–)20–55 cm long. Tepals 10–18 mm long. Filaments 2–2.5 mm long; anthers 3.5–4.5 mm long. Capsules irregularly globose, showing the outline of the seeds, (2.5–)4–6.8 mm long, seeds rarely more than 3 per locule; seeds 1.8–2.7 mm long, irregularly globose with a concave chalazal end, reddish brown to black (? with age), strongly rugose. Chromosome number $2n = 12$.

Eleutherine bulbosa is widespread, extending from southeastern Brazil and Bolivia to Venezuela and the West Indies (Fig. 4). The original habitat is uncertain. The most consistently fertile plants we have seen are from a population in the eastern Andean foothills of Peru, but occasional plants with capsules are known from eastern Brazil (Pará), Trinidad, Guadeloupe, and Santo Domingo. The branched inflorescence and, when present, the small, more or less globose capsules distinguish the species from its close relative *E. latifolia*. In its extended and branched inflorescence, we assume *E. bulbosa* is the less specialized species. The flowers of the two are essentially identical.

The several specimens sampled cytologically (see discussion of cytology), all sexually sterile, have the two long chromosomes heteromorphic and heterozygous for a pericentric inversion and a tandem duplication, which accounts for the prevalent re-

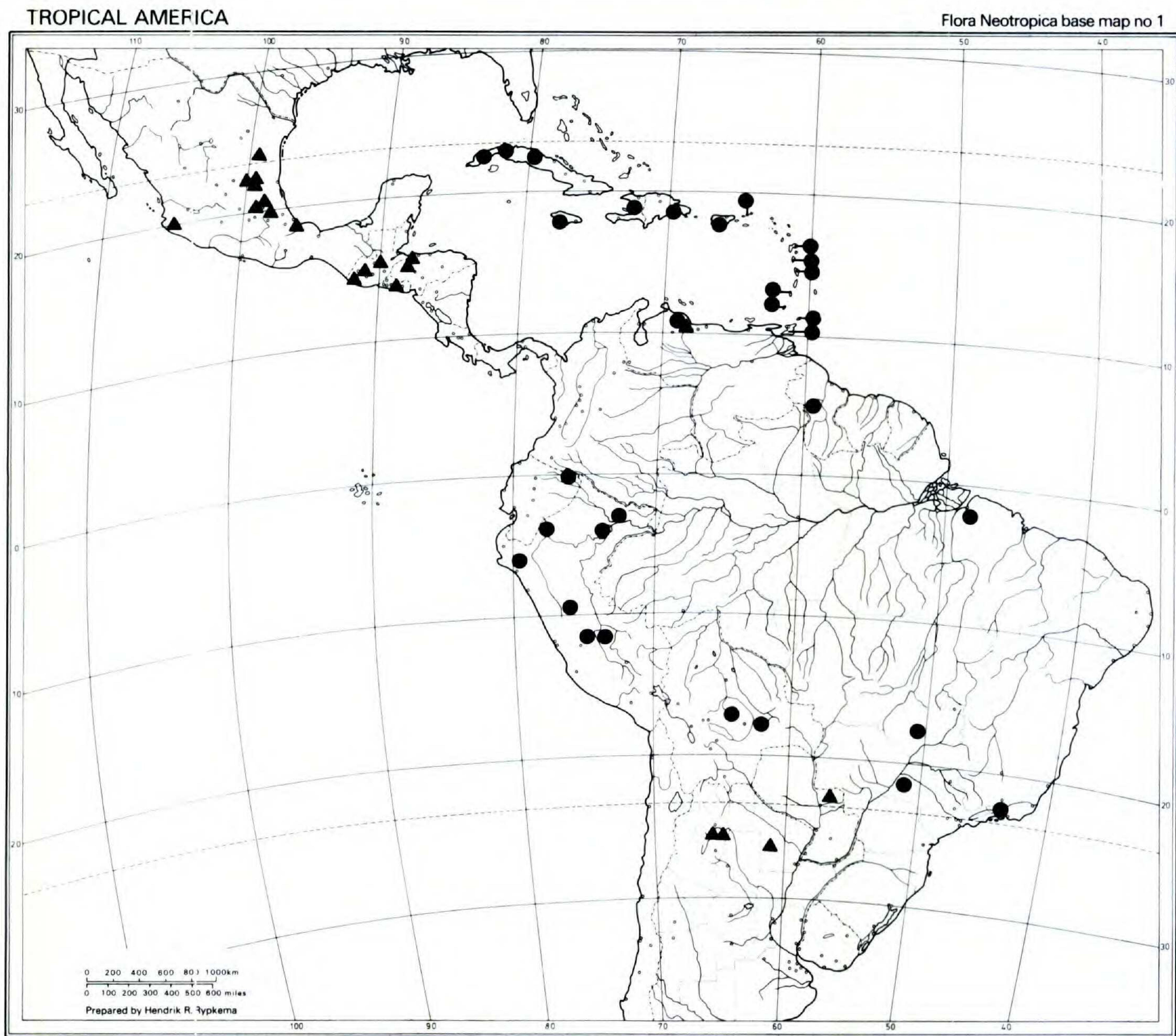


FIGURE 4. Distribution of *Eleutherine latifolia* (triangles) and *E. bulbosa* (circles).

productive sterility. Chromosomes have not been examined in any fertile plants.

Nomenclatural history. The systematics of this relatively uniform species is remarkably complex. Although first described by Phillip Miller in 1768 in the genus *Sisyrinchium*, his epithet was overlooked by Aublet (in 1775), who named the plant *Ixia americana*, and by Swartz, who gave it two epithets, *Sisyrinchium latifolium* in 1788 and *Moraea plicata* in 1797. All three species were based on the same type. Herbert's (1843) *Eleutherine anomala* was based on plants grown in Britain. Herbert was aware of the four earlier epithets for the species and regarded *E. anomala* as distinct from them. Herbert provided a generic name for plants that had until 1843 been assigned to no less than five genera, if Salisbury's nomen nudum for

the genus, *Galatea*, is included. Curiously, Herbert designated *Marica plicata* as the type of *Eleutherine* but did not make the combination *E. plicata* often attributed to him. Adding to the complexity is Lamarck's use of Linnaeus's *Sisyrinchium palmifolium* for *E. bulbosa*. *Sisyrinchium palmifolium* must be based on a specimen collected by Ardouin in Brazil (a species of *Sisyrinchium* still known by this name) rather than on the figure of *E. bulbosa* in Burman's *Plantae Americanae* that Linnaeus cited with a query, in the protologue of *S. palmifolium*. Lamarck's use of the epithet *palmifolium* for *E. bulbosa* was followed by Jacquin (1790), who referred the species to the African *Moraea*, and Merrill (1912), among others.

In 1934, Gagnepain described two more *Eleutherine* species from Indochina that are obviously forms of *Eleutherine bulbosa*: *E. subaphylla*, which

lacks foliage leaves; and *E. longifolia*, which lacks flowers. Specimens matching both are routinely encountered in herbarium material from the Americas, sometimes from populations that include plants of more normal appearance.

Eleutherine bulbosa is an important element of American Indian pharmacopeia and is one of few neotropical Iridaceae with known medicinal uses (Schultes, 1990). It is often cultivated in gardens maintained by Indian tribes (W. Lewis, pers. comm.) and is also fairly widely grown in the tropics as an ornamental. It is used as a vermifuge in Ecuador (Vickers & Plowman, 1984) and is widely documented in the literature and in herbaria as a treatment for bloody diarrhea (Ayala, 1984), haemorrhagia and open wounds (Lewis *et al.* 1966, 10624; Costa 164; Peters & Padoch 137; Hahn & Tredwell 125), and even as a contraceptive (Schunke 971). *Eleutherine bulbosa* is now naturalized in the Philippines and Indochina and cultivated in Kwazulu, South Africa (A. Hutchings, pers. comm.), where it is also used medicinally. Quisumbing (1951) recorded the use of *E. palmifolia* (i.e., *E. bulbosa*) as a diuretic in the Philippines. It is also believed to have magical and hallucinatory properties. Schultes (1990) has provided information about chemistry and possible active principles, so far hardly investigated.

2. *Eleutherine latifolia* (Standley & Williams)

Ravenna, *Phytologia* 56: 195 (1984). *Cipura latifolia* Standley & Williams, *Ceiba* 1: 75 (1950). TYPE: Honduras, El Zamorano, grounds of the Escuela Agrícola Panamericana, 14 Aug. 1947, *Molina* 498 (holotype, EAP). Figure 2B.

Eleutherine citriodora (Ravenna) Ravenna, *Phytologia* 56: 195 (1984), syn. nov. *Eleutherine bulbosa* subsp. *citriodora* Ravenna, *Bol. Soc. Argent. Bot.* 10: 314 (1965). TYPE: Argentina, in pratis urbi Tucumán, Feb. 1964, *Vervoorst s.n.* (holotype, Herb. Ravenna 285 n.v.).

Plants (6–)12–20 cm high, other characters as for the genus except the following. Inflorescence of one, rarely two, subsessile or stalked rhipidia borne in the axil of the cauline leaf; peduncle 10–50(–80) cm long; spathes 15–20 mm long. Tepals 12–14 mm long, 6–8 mm wide. Filaments 2.5–3 mm long; anthers 3 mm long. Style ca. 2 mm long, the branches ca. 4 mm long. Capsules obovoid to oblong-cylindric, 10–28 mm long, with numerous seeds per locule; seeds 2.1–2.3 mm long, conical, the sides somewhat flattened, lightly rugose, dull greenish yellow, dark brown at the chalazal end. Chromosome number $2n = 12$.

Eleutherine latifolia is widespread but scattered in the Neotropics and subtropics, with centers in northern Central America and Mexico and in southern South America, northern Argentina, Paraguay (Fig. 4), and according to Ravenna (1984a), Bolivia, but also recorded in Venezuela. The species is strongly autogamous. Because of the inflorescence that comprises one or occasionally two rhipidia, compared with the several in pseudopaniculate arrangement in *E. bulbosa*, we consider *E. latifolia* to be more specialized.

Until now, *Eleutherine latifolia* has been regarded as a Central American–Mexican endemic. However, the differences between this and the southern South American *E. citriodora* seem to us too trivial to merit continued separation. Herbarium specimens cannot as a rule be distinguished, although Central American plants are often sturdier. In cultivated samples of single populations from Mexico and from Argentina we noted that the Mexican plants have firmly erect stems, clear green foliage, and flowers lightly acrid-smelling, slightly smaller, and opening earlier in the evenings than the plants from Argentina. The latter have stems that seldom remain erect as the capsules develop, the leaves have a slightly bluish tinge and the flowers, faintly sweet-scented, open a full hour later than the Mexican plants, 6:00–6:30 P.M., and last about an hour later, till nightfall, 8:00–8:30 P.M. We have no information on interpopulational variation (flowers are rarely preserved in dry specimens and floral odor is never recorded) in either of the two main centers of the species nor in plants from Venezuela. Thus, at least on available information, we recommend including *E. citriodora* in *E. latifolia*. The only realistic way to tell the two apart is to know their geographic origin. The differences enumerated above are cryptic and can only be seen in live plants: even then we do not know how consistent they are across populations. Experience in other Iridaceae is that flower size, odor, and phenology will often vary to some extent in widely distributed species.

When Ravenna described *Eleutherine citriodora* as *E. bulbosa* subsp. *citriodora*, he distinguished it from subspecies *bulbosa* by its somewhat larger rhipidial spathes crowded in the axil of the cauline leaf; the oblanceolate, more acute, tepals; the flowers citrus-scented; and the stamens often suberect. This distinction is the same as that between the Central American *E. latifolia* and *E. bulbosa*, except for the sweet floral scent in so-called *E. citriodora* from Argentina. We have not seen the type of *E. citriodora*, which is in the private collection of P. Ravenna and is unavailable

for study. Our interpretation of the taxon is therefore based on the diagnosis and the locality information. The type collection was made near the town of Tucumán, northern Argentina, where plants corresponding to *E. latifolia* are well known, whereas *E. bulbosa* does not occur in Argentina. Unlike the closely related *E. bulbosa*, there are no recorded human uses of *E. latifolia*.

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